

A CYTOGENETIC STUDY OF GROWTH HABIT, SPELTOIDY AND AWNING
IN A MUTANT INDUCED BY 2,4-D IN THATCHER WHEAT

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A CYTOGENETIC STUDY OF GROWTH HABIT, SPELTROIDY AND AWNING
IN A MUTANT INDUCED BY 2,4-D IN THATCHER WHEAT

A DISSERTATION

SUBMITTED TO THE SCHOOL OF GRADUATE STUDIES
IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE
OF MASTER OF SCIENCE

FACULTY OF AGRICULTURE
DEPARTMENT OF PLANT SCIENCE

by

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EDMONTON, ALBERTA,

APRIL 1956

TABLE OF CONTENTS

	Page
1. INTRODUCTION	1
2. REVIEW OF LITERATURE	1
(a) Growth Habit	1
(b) Speltoidy	3
(c) Awning	9
(d) Behavior of terminally deleted chromosomes	13
3. MATERIALS AND METHODS OF PROCEDURE	15
(A) ORIGIN AND DESCRIPTION OF MATERIALS	15
(a) Origin	15
(b) Description of Materials	15
(i) Mutant	15
(ii) Thatcher	15
(iii) Thatcher monosomic IX	16
(B) EXPERIMENTAL METHODS	16
(a) Crosses	16
(i) Mutant x Thatcher	16
(ii) Thatcher mono IX x Mutant	16
(b) Cytological studies	19
(i) P.M.C. Cytological observation	19
(ii) Root tip Cytological observation	19
4. EXPERIMENTAL RESULTS	20
(A) CROSSES	20
(a) Mutant x Thatcher	20
(b) Thatcher monosomic IX x Mutant	22
(B) CYTOLOGICAL STUDIES	23
(a) P.M.C. Cytological observation	23
(i) Thatcher	23
(ii) Mutant	23
(iii) F ₁ Late Spring	23
(iv) F ₂ Segregants	24
(v) Thatcher monosomic IX	25
(vi) F ₁ Late Spring from Mono	25
(vii) F ₁ Winter def Mono	25
(b) Root tip cytological observation	28
5. DISCUSSION	36
(a) Crosses	36
(b) P.M.C. Cytological studies	36
(c) Root-tip cytological studies	42
6. CONCLUSION	43
7. SUMMARY	44
8. ACKNOWLEDGEMENTS	45
9. REFERENCES	46

LIST OF TABLES

	Page
1. F_2 segregation in the cross Mutant x Thatcher	21
2. F_1 segregation in the cross Thatcher mono IX x Mutant	22
3. Chromosome behavior in P.M.C. Cytological Studies	27

LIST OF FIGURES

1. Diagrammatic Representation of Crosses with Respect to Genes and Chromosomes	41
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LIST OF PLATES

1. Morphology of Plants	29
2. Representative Plants of P, F_1 and F_2 of the cross Mutant x Thatcher, when all Plants had Headed	30
3. Representative Spikes of P, F_1 and F_2 of the cross Mutant x Thatcher	31
4. Chromosome Behavior at M1 in Mutant and F_2 Winter	32
5. Chromosome Behavior at M1 in F_1 Late Spring, F_2 Late Spring and F_1 Late Spring from Mono	33
6. Chromosome Behavior at M1 and A1 in F_1 Winter def Mono	34
7. Chromosome Morphology and Count in Root Tip of Mitotic Metaphase	35

ABSTRACT

A Cytogenetic Study of Growth Habit, Speltoidy and Awning in a Mutant Induced by 2,4-D in Thatcher Wheat

A cytogenetical study was made of a mutant characterised by winter growth habit, extreme speltoidy and full awning. This mutant was found as segregant in the T_2 progeny of T_1 Thatcher wheat seedlings treated with 2,4-D. The other segregants in the same progeny were normals and late speltoids.

Two crosses were made

- (1) Mutant x Thatcher
- (2) Thatcher monosomic IX x Mutant

Cytogenetical analysis confirms previous findings that genes affecting speltoidy, awning and habit of growth are on the long arm of chromosome IX.

The Mutant is homozygously deficient for most of the long arm of chromosome IX, and this loss is correlated with the winter growth habit, extreme speltoidy and full awning of the spike.

This deficiency was easily distinguished cytologically in pollen mother cell studies but it was not possible to identify the deficient chromosome in root tip studies since the deficiency was not extensive enough to produce a telocentric chromosome.

The mutant is probably the closest approach so far recorded of a wheat plant that effectively is homozygous for the short arm of chromosome IX in Thatcher.

INTRODUCTION

In a polyploid species such as wheat, viable plants with chromosome aberrations involving deficiency of a portion of a chromosome, or complete loss of one or even of a pair of chromosomes, provide a basis for cytogenetical analysis that permits the association of genes with certain chromosomes.

The present study consists of a cytogenetical analysis of a mutant obtained from 2,4-D treated wheat seedlings.

2. REVIEW OF LITERATURE

(a) Growth Habit

Early work on inheritance of growth habit (1, 7) show that spring habit is dominant to winter habit of growth, and simple ratios were obtained in segregating generations. Although later studies (2, 8, 9) confirmed that spring habit is dominant or partially so, these workers found that the inheritance of growth habit was controlled by multiple genes, and no attempt was made to determine the number of gene pairs involved. Powers (16) postulated that three major gene pairs of unequal effect regulated habit of growth and earliness.

Literature on the use of aneuploid lines in the cytogenetical analysis of growth habit is scanty. Sears (17) recorded delayed maturity in Chinese Spring aneuploid lines Nulli V, VIII, IX, XVI, XVIII and mono IX and XVIII.

Unrau (23) studied segregation for growth habit in F_2 and F_3 populations from the crosses of variety Hymar, a winter wheat, on seventeen different monosomic lines of Chinese Spring. The F_2 results, except those involving chromosome IX closely fitted a ratio of 15 spring : 1 winter indicating that duplicating genes conditioned habit of growth in these crosses. In F_3 a close fit to the expected ratio of 7 homo spring : 8 segregating lines : 1 homo winter was obtained.

Segregations in F_2 and F_3 populations involving chromosome IX were distinctly different from those observed in other lines and combined data from F_2 and F_3 lines involving chromosome IX gave a good fit to a 3:1 ratio. Unrau postulated that one of the duplicate genes conditioning habit of growth in the crosses must be carried by chromosome IX.

Sears (20) affirmed that mono IX and mono XVIII lines are distinctively late maturing compared to the other lines and observed late maturity in nulli II, VIII, XVI, XVIII and in mono V, IX and XVIII. Sears (19, 20) working on plants possessing telocentric chromosomes was assured that certain spring growth habit genes are located on the long arm of chromosome IX and mono telo XVIII resembled the normal monosomic in being somewhat late.

(b) Speltoidy

A detailed account of the various speltoids has been presented by Smith et al. (21) while a comprehensive literature review of the speltoidy problem has been made by MacKey (14). In the light of all available knowledge up to the present time it is interesting to trace the development of thought on the subject and the various hypotheses put forward.

The various speltoids have been classified into several genetic types by different workers but Nilsson-Ehle's original classification (1921) has usually been cited by several authors, (11, 12, 13, 14, 21). He is said to have classified his speltoids into three series according to the type of segregation of self fertilized heterozygous forms

Series	Normal	:	Het Speltoid	:	Hom Speltoid
A	1	:	$< 2 - 1 >$	:	$< 1 - 0$
B	1	:	3.5 - 10	:	< 0.1
C	1	:	≤ 1	:	≤ 0.2

Deviations in series A are said to be due to varying degrees of failure of speltoid enhancing pollen to function in fertilization.

In series B the speltoid enhancing pollen almost never functions. Furthermore speltoid enhancing ovules must be produced in great excess, while in series C non-functioning of speltoid enhancing pollen and the production of slightly more normal than speltoid bearing ovules are presumed to account for such a progeny ratio.

Nilsson-Ehle apparently had difficulty in assigning some strains to one of the two series A or C owing to deviation of progeny ratios. Zygotic elimination of het-speltoids could play some part in determining the fluctuations and allow an excess of normals when plant mortality is high, (12, 13). Huskins et al. (12, 13, 21) have classified the speltoid series A,B,C as α , β and γ in order to avoid confusion with chromosome symbols. They have classified all speltoids that give ratios close to 1N:1 het spelt, with very few or no homo speltoids as series γ , and only those that produce an appreciable number of progeny of nearly or quite normal vigour as series α . Genetic and cytological data give a better fit with this classification. However, Huskins et al. (12,13,21) stressed that there are intergrading types and that the distinction between series α and γ speltoids was one of degree only.

Huskins' citations (11, 12, 13) of Linhard's hypothesis (1922) and Winge's development of the hypothesis are as follows: Speltoids and related aberrant forms arise through chromosomal irregularities, Linhard (1922). This was developed by Winge (1924) on the basis that the cultivated wheat, T. Vulgare is a hexaploid species and assuming that its 21 chromosome gamete consisted of three more or less similar sets of 7. In view of this situation faulty conjugation could occur.

Winge represented $\frac{ABC}{ABC}$ as the normal triplicated set of chromosomes among which the C chromosomes were postulated to carry genes pushing development towards the compactum type and the B chromosomes to carry genes tending towards speltoidy.

An excess of B chromosomes or a deficiency of C chromosomes would then produce speltoids and, if vice versa, compactoids. The A chromosomes were not assigned with any function.

During normal meiosis A paired with A, B with B and C with C but in faulty conjugations, since it was presumed that the B and C genome chromosomes may pair occasionally, gametes such as ABB could arise and this when paired with a normal gamete would give rise to the zygotic formula $\frac{ABB}{ABC}$ representing a het speltoid. Such a heterozygous plant could give rise to various progeny ratios. He went even further to postulate that het speltoids with the formula $\frac{ABO}{ABB}$ and homo speltoids $\frac{ABO}{ABB}$ and $\frac{ABBB}{ABB}$ could occur. However he was unable to confirm his hypothesis with cytological evidence.

Cytological studies of speltoids were made by Huskins (11) on the α , β and γ series speltoids obtained from Nilsson-Ehle and Akerman.

Type α speltoids were found to have the normal chromosome number of 42 but unusual chromosome arrangements occurred. Heterozygous speltoids of this type were characterised by the presence of a trivalent and a univalent in their pollen mother cells. Homozygous speltoids were characterised by a quadrivalent.

The β type speltoids were found to possess only 41 chromosomes which were regularly arranged as 20 bivalents and one univalent ($20^{II} + 1^I$). These plants formed more 20 chromosome gametes than 21 chromosome gametes due to frequent loss of univalent chromosomes during meiosis.

Furthermore there must have been differential gametic viability and zygotic elimination governed by chromosome number. The weak homozygous segregates of this type were presumed to have only 40 chromosomes.

In the C type speltoids, the heterozygotes were found to possess 43 chromosomes which were usually arranged as 20^{II} and 1^{III}. Huskins (11) presumed that the C type ratio was due to the 43 chromosome heterozygotes forming more 21 chromosome than 22 chromosome gametes and that it was modified by differential gametic viability and zygotic elimination similar to that in type B. A homozygous speltoid of type C was found to have 44 chromosomes.

At that time Huskins (11) concluded that speltoids arose from normal wheat plants through chromosomal aberration, and that the different ratio types were determined primarily by differences in chromosome number.

The use of aneuploid lines of wheat in genetical analysis has greatly facilitated the location of genes on the chromosomes. The speltoid character has consistently been shown to be regulated by a particular pair of chromosomes denoted as IX by Sears (17) previously described as C by Winge (1926). Mono IX belongs to the B speltoid. Nulli IX has been described as Homozygous speltoid, culms and leaves narrow, nonpubescent nodes, maturity delayed, spikes lax and narrow, glumes small and stiff, awns somewhat increased in length, male sterile, Sears (17) further adds "the factors for pubescent nodes, squareheadedness and suppression of speltoidy already known to be linked together on the speltoid chromosome, prove to be located on the chromosome here designated IX".

Morphologically the centromere of chromosome IX is sub median. The long arm is marked by a secondary constriction about three-eighths along its length. From various experiments it is concluded that the speltoid gene Q and beard gene B₁, are located on the long arm of chromosome IX since γ het speltoids arise through loss of all or part of the long arm, (21). The segment of genes B₁ - Q is believed to be interstitial in the distal segment since chromosome configurations in het speltoids lacking part of the long arm demonstrate the deficiency, (21). They also conclude that the extent of loss determines the degree to which chromosome behaviour is affected in meiosis and also the extent to which mutant pollen is handicapped in competition with the normal in het speltoids. Furthermore the genes B₁ and Q are ascribed to have inhibitory or suppressive functions. The "positive" speltoid and awn genes have yet to be located.

MacKey (14) refers to no less than seven distinctly different suggestions that have been put forward from time to time, for explaining the deficiency type of speltoidy. These explanations all based on spontaneously occurring material are:

- (a) Fragmentation followed by a simple deficiency
- (b) Substitution of chromosomes
- (c) Deficiency duplication
- (d) Gene mutation
- (e) Aneuploidy
- (f) Duplication through the production of isochromosomes
- (g) Position effect

Of all of the above hypotheses the deficiency hypothesis is the only one conclusively proved as one explanation from the results obtained in neutron and X-ray experiments (14).

Even then, considering the mode of action of X-rays and neutrons, MacKey (14) does not believe that the mere existence of a heteromorphic bivalent or two univalents of unequal size in certain metaphase I of the het-speltoid is sufficient to prove that a simple deficiency is the initial cause of the mutation since chromosome substitution as well as deficiency duplication may result in similar heteromorphic 1^{II} or 2^I . In X-ray and neutron experimental material, (14), there appeared in some of the induced speltoids ($1^{III} + 1^I$) and 1^{IV} in addition to 1^{II} and 2^I configurations. MacKey (14) postulates that, should the high frequency of multivalents be really closely associated with the speltoid character, then deficiency-duplication must be the only or at least the most important explanation.

MacKey's diagram (14) of a translocation followed by a deficiency duplication is in conformity with his results on het and hom speltoids as well as het and hom compactoids all with $2n = 42$ and which show an abnormally high frequency of 1^{IV} and (1^{III} and 1^I).

In the speltoid problem therefore the predominant causes are simple deficiency and possibly deficiency duplication. However other causes of mutation cannot be completely rejected. The differences in the speltoids of $2n = 42$ chromosome genetic constitution seems to depend on the extent of variation in the size of deletion in the long arm of chromosome IX and the effect of this deletion on the competitive ability of the pollen. The egg may tolerate such deficiency.

(c) Awning

Awning in wheat varies from awnless through tip-awned to fully awned varieties. The mode of inheritance is known for specific crosses but it is difficult to correlate the various data since no standard awn classification system has been used nor is distinction made in all cases of genotypic or phenotypic crosses. Awning has been associated with conflicting results on yields, (3, 4, 5) while on the other hand also with the undesirable characteristics of speltoid mutations (refer review on Speltoidy).

Extensive studies on awning by Watkins and Ellerton (25) indicate that awn length in wheat is affected by both major and modifying genes, as well as by chromosome number. They propose that there may be three or possibly four main loci affecting length of awn and on this basis established the genes A, B_1 and B_2 and the respective recessive allelomorphs that affect awn length. Another gene Hd reduces the length of the awns and generally makes them curved and twisted near the base especially on late tillers. They postulated the genic constitution of bearded wheats as $b_1b_1, b_2b_2, hd\ hd$.

Tipped I	as $B_1B_2b_2b_2$
Tipped II	as $b_1b_1B_2B_2hd\ hd$
Hooded	as $b_1b_1b_2b_2Hd\ Hd$
and Beardless	as $b_1b_1B_2B_2Hd\ Hd$

Other combinations of the same genes may be responsible for the wide variation in awning.

Since the establishment of aneuploid lines in wheat (17) and use of these lines in cytogenetic studies, a great deal of information has been forthcoming some of which substantiate the postulations of Watkins and Ellerton (25).

Sears (17) reports the following in the common wheat variety, Chinese Spring.

- (1) the recessive gene b_1 on chromosome IX, inhibits awns to a lesser extent than its dominant allele B_1
- (2) chromosome X carries an active awn suppressing gene B_2
- (3) Chromosomes II and XX carry genes promoting awn length
- (4) a hooded factor Hd on chromosome VIII shortens and re-curves awns

O'Mara (15) reported that Marquis wheat carried a strong awn inhibitor B_1 on chromosome IX.

Unrau (23) using Chinese Spring monosomics and nullisomics in the analysis of Federation 41 and Hymar, of which Hymar and Chinese Spring are almost awnless, suggested on the basis of F_2 data that awning in this cross was apparently conditioned by three genes. Recessive alleles of the two dominant awn inhibiting genes of Chinese Spring were associated with chromosome VIII and X of Hymar. A dominant awn-inhibiting gene with greater effect than either of the two Chinese Spring awn inhibitors was associated with IX of Hymar. Unrau added that these results supplement the finding of Sears (17) and O'Mara (15).

Heyne and Levers (10) using Chinese Spring monosomics in the analysis of Pawnee, an awned hard red winter wheat variety, concluded that the recessive alleles hd , b_1 and b_2 are located on chromosome VIII, IX and X respectively, while the recessive factors for promoting awn growth are apparently on chromosome II and XX as in Chinese Spring. However chromosomes XII, XVI and XXI also seem to be involved in awn expression although this was not expected on the basis of published information available until that time.

Therefore they proposed a series of "A" genes. Since they believed that it has been well established that Chinese Spring has incompletely dominant, incompletely epistatic awn inhibitors Hd and B_2 on chromosomes VIII and X respectively and that the absence of Hd and B_2 genes enhances awn development rather than the presence of the recessive alleles hd and b_2 .

Hypothetically the "A" gene is non epistatic, but incompletely dominant over an awn producing allele a . In the homozygous condition (aa) full awns could be produced theoretically, if not inhibited by partially epistatic genes Hd or B_2 .

While assigning recessive genes a_1 and a_2 to chromosomes II and XX of Chinese Spring and which are reported to have an awn stimulating effect, (17) similar genes may be assigned to chromosomes XII, XVI and XXI of Pawnee.

The genotypes of Pawnee and Chinese Spring would then be:

Chromosome	VIII	X	XII	XVI	XXI
Chinese	Hd	B ₂	A ₃	A ₄	A ₅
Pawnee	hd	b ₂	a ₃	a ₄	a ₅

This hypothesis satisfied the findings in their experiment using monosomic analysis.

Heyne and Levers (10) therefore suggest that this awn theory may be modified considerably and yet retain its essential principles and they believe that this or some other multiple-gene theory is quite necessary to explain the occurrence of awned types in so many different crosses with monosomic stock while they assert that this is an extension of, rather than a contradiction of previous ideas.

(d) Behavior of Terminally Deleted Chromosomes

The cytology of heterozygous speltoids of series γ obtained from Akerman 1926 had been studied by Smith et al., (21) since 1926. In certain of these speltoids which had 42 chromosomes one heteromorphic bivalent was usually observed. The chromosomes involved were associated loosely in most cells while in some they unassociated during metaphase I. The larger member when unassociated was similar in form to the univalent chromosome of β het speltoids. The shorter member was three quarters as long as the other member of the heteromorphic pair. The pairing relationship indicated a deficiency distal to the secondary constriction of the long arm of chromosome IX.

Sometimes during Anaphase I the two unassociated univalents moved on to the equatorial plate and split as univalents do. This occurrence explains the possibility of obtaining a few het speltoids of 41 chromosome constitution from plants having 42 chromosomes of which one pair was heteromorphic. Failure of unassociated chromosomes during Metaphase I to be included in the first or second division nuclei could give rise to speltoids of three chromosomal types, $40 + 2 \text{ Cd}$, $40 + 1 \text{ Cd}$ and 40 where Cd represents the deficient chromosome.

Various types of chromosomal configurations were observed in 42 chromosome speltoids, ranging from apparently normal 21^{II} through a high frequency of interlocking of certain pairs at Metaphase I or $(20^{\text{II}} + 2^{\text{I}})$ or $(19^{\text{II}} + 1^{\text{III}} + 1^{\text{I}})$ or $(19^{\text{II}} + 1^{\text{IV}})$ to $(19^{\text{II}} + \text{other configurations and fragments})$.

Sears (18, 19, 20) described the mode of origin and behavior of telocentric chromosomes involving the long arm chromosome IX of Chinese Spring. Misdivision of univalent mono IX chromosomes at T1 resulted in the production of telocentrics. A telocentric may be considered as a chromosome deficient for one entire arm.

A pair of homologous telocentric chromosomes or even a telocentric chromosome with its normal homologue possessing both arms, went through meiotic divisions in normal fashion. Occasionally the two homologous telocentrics or the telocentric and its normal homologue were found unpaired at metaphase I. Decreased likelihood of chiasma formation in the relatively short telocentric chromosome may be the cause for unpairing in these chromosomes concerned. A single univalent telocentric behaved very much like a monosomic univalent. Isochromosomes were probably formed by reduplication of a telocentric arm.

In somatic tissue complete loss of telo IX had been observed in several instances especially in chimera sectors. Sears (19) suggested that many of the chimeras observed in wheat by several investigators were due to somatic loss of telo IX.

3. MATERIALS AND METHODS OF PROCEDURE

(A) ORIGIN AND DESCRIPTION OF MATERIALS

(a) Origin

Several true breeding plants of winter growth habit segregants in the T_2 generation from T_1 plants of Thatcher wheat seedlings treated with 2,4-D (Unrau and Larter, 1952), together with parental Thatcher seeds and Thatcher mono IX seeds, were obtained. The other segregants in the T_2 generation were normals and late speltoids.

(b) Description of Materials

(i) Mutant

The Mutant used was readily identifiable in the field among the other segregants by its prostrate winter habit vegetative growth and from the absence of any signs of heading even after more than three months of very favourable summer conditions. It bred true and took more than four months to head when sown directly as seed in the greenhouse. The head is characterized by extreme speltiness, full awning and slenderness. This mutant shall henceforth be referred to as "Mutant".

(ii) Thatcher

The variety Thatcher is a hard red spring wheat. The spike is fusiform, apically awned. The straw is medium long and strong (1954). It takes about 65 days to head.

(iii) Thatcher monosomic IX

Thatcher mono IX is readily identified in the field by a delay of almost three weeks in heading and a slight increase in height as compared to the other monosomic lines or normal Thatcher. Tillering is more pronounced than in Thatcher. The spike is characterized by a slight increase in length tapering towards a non-compact tip, and is speltoid and short awned.

(B) EXPERIMENTAL METHODS

(a) Crosses (i) Mutant x Thatcher

(ii) Thatcher mono IX x Mutant

The Mutants were transplanted from the field into the growth chamber and greenhouse in the late autumn of 1954 for breeding and crosses. They headed as expected having received the cold shocks of late autumn in the field. They were all crossed with Thatcher pollen. Because of poor pollen production, only ten seeds were obtained from three different plants. These ten seeds together with seeds of parents for checks were germinated in moist sand in petri dishes.

The F_1 and the mutant seeds did not germinate probably, because of post harvest dormancy. They were therefore put in the cold room at $0^\circ - 1^\circ$ C. while the seed were still moist for a week, to break this dormancy and then taken out for germination at room temperature. All the seeds germinated and when their radicals had just emerged they were placed once again in the cold room for thirty days for vernalization at $0^\circ - 1^\circ$ C. They were then planted in soil in the benches in the greenhouse, expecting to obtain F_2 seeds for summer planting in the field.

These vernalised seedlings took more than seventy days to head. The seeds did not mature in time to sow in the field in summer. Therefore sowing of F_2 seeds had to be done in the green house in the winter of 1955.

Meanwhile, as there were only ten F_1 seeds from the Mutant x Thatcher cross, five plants from each line of the vernalised 70 day-old mutant plants of check rows grown in the green house were transplanted in pots and kept there for hardening. They were then chilled in a cold chamber for two weeks at $0^{\circ} - 1^{\circ}\text{C}$ after which they were planted out in the field in the spring so that crosses with Thatcher and Thatcher mono IX could be made. This was a success and a great number of F_1 seeds were obtained for cytogenetical analysis and for sowing together with F_2 seeds obtained from the F_1 plants of the previous cross.

When all the necessary seeds for final analysis were obtained the sowing was done in two stages.

Stage I; Seeds used were:

P	Mutant
P	Thatcher
F_1	Mutant x Thatcher
F_2	F_1 Mutant x Thatcher

As a preliminary dormancy test a few seeds of each parent line were grown in moist sand in petri dishes. The mutant, F_1 and F_2 seeds did not germinate and were therefore given a cold treatment as previously mentioned for post harvest dormant seeds, after which all of them germinated at room temperature.

The remaining portion of the seed stocks were given a similar cold treatment and sown without any vernalisation, in head progeny rows in the green house.

The morphological characters of these plants and spikes were observed, classified and photographed.

Stage II; Seeds used were:

P	Mutant
P	Thatcher
P	Thatcher mono IX
F ₁	Mutant x Thatcher
F ₁	Thatcher mono IX x Mutant

The seeds were germinated on gauze spread tightly on a wooden frame and set afloat in a pan of water so that the gauze was always moist. The seedlings were numbered according to point of location. In order to break winter dormancy the pan with its contents were put in the cold chamber for a week at 0° - 1°C. It was then taken out and the seeds germinated in room temperature.

Root tips were excised, numbered, pretreated in a saturated solution of paradichlorobenzene for six hours and then fixed in Farmers fluid and later transferred to 70% alcohol.

The seedlings were planted in pots and numbered, so that data from cytological analysis of root tips could be correlated with morphological characteristics.

The morphological characters of these plants and spikes were studied, classified and photographed.

(b) Cytological studies

(i) P.M.C. Cytological observation

All available P.M.C. material of parents, F_1 and F_2 were collected and fixed in Carnoy's Fluid, later transferred to 70% alcohol. Chromosome squashes were prepared using the acetocarmine stain technique outlined by Smith (1948). Temporary slides were made by sealing the cover slips with 10% glycerol. Chromosome counts were made and chromosome morphology and configurations at all stages of meiosis especially of metaphase I were closely observed, recorded and photographed.

(ii) Root tip cytological observation

Chromosome squashes were prepared by pretreating the root tips from 70% alcohol with hydrolysing fluid containing 1 conc Hcl : 1 95% alcohol followed by washing in 70% alcohol before staining with hot acetocarmine. Temporary slides were made by sealing the cover slips with 10% glycerol. Chromosome counts were taken, and chromosome morphology and configurations were studied, recorded and photographed.

EXPERIMENTAL RESULTS

(A) CROSSES

(a) Mutant x Thatcher

All the F_1 of this cross were intermediate with respect to heading when compared with the parents, being more than two weeks later in heading than Thatcher and very much earlier than the mutant.

The spikes of the F_1 plants appeared intermediate to that of the mutant and Thatcher parents. The spikes were as speltoid as those of the mutant, quite long, with about four basal spikelets sterile as the mutant parent. Awning was similar to Thatcher.

The F_1 of this cross will in future be referred to as F_1 Late Spring.

The F_2 segregated into four easily identifiable and distinct types as follows:

- (1) Spring Thatcher type Segregates - F_2 Spring
- (2) Late Spring F_1 type segregates - F_2 Late Spring
- (3) Mutant type segregates - F_2 Winter
- (4) Weak spindly type segregates - F_2 aberrant

These segregates will henceforth be referred to as F_2 Spring, F_2 Late Spring, F_2 Winter, F_2 Aberrant respectively.

The F_2 Spring segregant was the first to head at about the same time as Thatcher checks. The spike resembled that of Thatcher in all characters.

About a week after the last F_2 Spring segregate has headed the F_2 late Spring segregant began to head. The spike was very similar to that of the F_1 Late Spring.

The F₂ Winter, the third type of segregant was distinguishable from the other two mentioned segregants by the very pronounced vegetative character similar to the mutant parent. These plants headed about five weeks after most of the F₂ Late Spring plants had headed. The spike was indistinguishable from the spike of the mutant parent.

These three types of segregants were expected theoretically. However, there were eight plants not in this category, that were weak and spindly. They were transplanted into pots for closer observation. Three of them grew vigorously. Two of these were classified as F₂ Late Spring and the third as F₂ Winter.

The other five remained weak and spindly and produced spikes that were small; each spike having only three or four spikelets which were sterile. The spikes resembled the weak and sterile spikes of very late tillers.

Four of these weak and spindly plants headed as early as F₁ or F₂ Late Spring types. One of the four may have involved a twin embryo since two shoots of similar size grew from the same seed. These two shoots produced spikes similar to the other small and sterile spikes and therefore the plant is included in this group. The fifth plant headed as late as the F₂ Winter. These five are classified as F₂ Aberrant.

The F₂ results are presented in Table I

TABLE I

F₂ segregation in the cross Mutant x Thatcher

Mutant Plant Cross	F ₂ Spring	F ₂ Late Spring	F ₂ Winter	F ₂ Aberrant	Total
1	53	90	10	3	156
2	40	39	3	1	83
3	69	80	13	1	163
Total	162	209	26	5	402

(b) Thatcher Monosomic IX x Mutant

The F_1 of this cross produced two types of segregants:

- (1) Late Spring Type - F_1 Late Spring from Mono
- (2) Mutant type - F_1 Winter def Mono

These two types of segregants will in future be referred to as F_1 Late Spring from Mono and F_1 Winter def Mono respectively.

(1) F_1 Late Spring from Mono

The F_1 Late Spring from Mono headed at the same time as the check plants of Thatcher mono IX, and F_1 Late Spring. The spike characters of these plants were indistinguishable from that of the F_1 Late Spring, F_2 Late Spring or Thatcher mono IX in shape, length, speltoidy and basal spikelet sterility.

(2) F_1 Winter def Mono

The other type of segregant, F_1 Winter def Mono did not head for quite a long time and was indistinguishable from the Mutant parent in heading dates or spike characters.

Segregation in F_1 of the cross Thatcher mono IX x Mutant are presented in Table (2).

TABLE 2

F_1 segregation in the cross Thatcher mono IX x Mutant

Cross	F_1 Late Spring from Mono	F_1 Winter def Mono	Total
Thatcher mono IX x Mutant	11	31	42

(B) CYTOLOGICAL STUDIES

(a) P.M.C. Cytological observation

(i) Thatcher

The behavior of 21 pairs of chromosomes appeared normal with regular formation of 21 bivalents at metaphase I, and of two groups of 21 dyads each at Anaphase I.

(ii) Mutant

In the mutant there were usually 20 regular bivalents at metaphase I but irregular behavior was observed in two chromosomes. These two chromosomes were similar in form in being comparatively short, straight and rod shaped. They usually appeared as an open bivalent or as two univalents but never as a closed ring bivalent at metaphase I, and when unpaired were frequently off the plate, and were therefore easily identified even when the rest of the chromosomes were in pairs or were clumped together. However, in most cases all the chromosomes including the two short chromosomes passed through meiosis in regular fashion.

(iii) F₁ Late Spring

Chromosome behavior in F₁ Late Spring was somewhat similar to that in the mutant parent where 20 pairs behaved in a regular manner while two chromosomes were irregular. But in this material the two chromosomes differed in morphology. One chromosome was short, straight and rod shaped as the irregular pair of chromosomes in the mutant and is presumed to be from the mutant, while the other chromosome was long and bent towards one end and is presumed to be from the Thatcher parent.

The two chromosomes usually synapsed at metaphase I forming a heteromorphic bivalent but sometimes were present as two univalents of dissimilar size and shape but never as a closed ring bivalent. They were frequently off the plate and were easily recognized even when the rest of the chromosomes were in pairs or were clumped together. All the chromosomes including these two chromosomes passed through meiosis in normal manner in most cases.

(iv) F₂ Segregants

Observation of chromosome behavior in the F₂ was made on the following segregant types:

F₂ Spring similar to that in Thatcher

F₂ Late Spring similar to that in F₁ Late Spring

F₂ Winter similar to that in the Mutant

Among the aberrant type of segregants two were examined cytologically, one which headed as early as the F₂ Late Spring and the other which headed as late as the F₂ Winter. Chromosome morphology and chromosome behavior in these two were similar to that observed in F₂ Late Spring and F₂ Winter respectively.

(v) Thatcher mono IX

At metaphase I the univalent mono IX chromosome was usually off the plate and easily recognized. At anaphase I it was fairly common to observe the univalent as a lone chromosome at the equatorial plate splitting itself or misdividing, while the other chromosomes had already moved towards the spindle poles. Sometimes the univalent dyad was included with one of the groups of 20 dyads. The other chromosomes passed through meiosis as usual. Micronuclei were frequently observed in tetrads.

(vi) F_1 Late Spring from Mono

Chromosome behavior in these late spring plants produced from Thatcher mono IX x Mutant cross was very similar to that of F_1 Late Spring or F_2 Late Spring segregants.

(vii) F_1 Winter def Mono

The behavior of the chromosomes in this type is not unlike that of Thatcher mono IX. As expected 20 normal bivalents and one short univalent which is presumably from the pollen of the mutant parent and easily recognized from the other chromosomes, were observed at Metaphase I.

At Anaphase I the univalent was either included with one of the groups of 20 dyads at either pole or was observed as a lone chromosome at the equatorial plate splitting itself. Micronuclei were frequently observed in tetrads.

Besides the irregular behavior of two chromosomes in the Mutant and Late Spring material, and expected behavior of the univalent chromosome in the monosomic plants, other chromosome configurations were observed occasionally or rarely in the mutant, F_1 and F_2 segregant material.

The configurations are as follows:

- 1) a trivalent and a univalent at MI
- 2) a quadrivalent at MI
- 3) four univalents at MI
- 4) six univalents at MI
- 5) one isochromosome and one univalent at MI
- 6) two lagging dyads at anaphase I

The data on chromosome behavior is presented in Table 3.

The key to this table is as follows:-

At Metaphase I

P = An atypical, open bivalent observed but no full count of the other chromosomes possible.

$20^{II} + P$ = 20 typical bivalents and 1 atypical open bivalent.

2^I = 2 univalents observed but no full count of the other chromosomes possible.

$20^{II} + 2^I$ = 20 typical bivalents and 2 univalents.

$19^{II} + 1^{IV}$ = 19 typical bivalents and 1 quadrivalent.

$20^{II} + 1^I$ = 20 typical bivalents and 1 univalent.

At Anaphase I

21 - 21 = 21 dyads in each of the two groups.

42 = 42 dyads at meta-anaphase I.

20 - 1 - 20 = 20 dyads in each of the two groups with one lone dyad at the equatorial plate.

The rare and irregular chromosome configurations are:-

At Metaphase I

1^{IV} = a quadrivalent.

$1^{III} + 1^I$ = a trivalent and a univalent.

4^I = four univalents.

6^I = six univalents.

$1^{iso} + 1^I$ = one iso and one univalent

At Telophase I

L = laggards.

The number of heads analysed are under the column H.

Chromosome Behavior in P.M.C. Cytological Studies

H Type	P	(20II+P) 2I	(20II+2I) (19II+1IV)	(21-21) 42 1IV	(1III+1I) 4I 6I	(1iso+1I) (2L)	Total
10 P. Mutant	157	7 97	1 1	2 1 3	- - -	7 -	276
5 F2 Winter	125	36 20	- 8	9 - -	- - -	- -	198
13 F1 Late Spring	103	7 86	- 4	5 9 -	1 1 1	2 1	219
19 F2 Late Spring	387	68 214	7 26	39 9 3	6 4 2	3 5	773
2 F1 Late Spring from Mono	130	25 39	12 -	3 - -	- - -	- -	209
H Type		1I (20II + 1I)	(20-1-20)	(1L)			
3 F1 Winter def Mono		143 19	6 18				186
					Total		1861

(b) Root-tip cytological observation

The chromosome numbers in root-tip studies were as follows:-

Type	Number
Thatcher	42
Mutant	42
F ₁ Late Spring	42
Thatcher Mono IX	41
F ₁ Late Spring from Mono	42
F ₁ Winter def Mono	41

However it was not possible to identify the particular short chromosome, which was easily identified in Metaphase I of pollen mother cell studies, since there were several chromosomes each with one short arm projecting beyond their centromeres. Furthermore it is certain that this short chromosome involved is not a telocentric chromosome.

Plate I. Morphology of Plants



1-a. Segregation in T₂ of T₁ speltoids induced by 2,4-D in Thatcher wheat seedlings. Note vegetative growth of Mutants among other segregants.



1-b. Difference in growth habit between Mutant and Thatcher sown on same day Summer 1955.
Left - Mutant
Right- Thatcher



1-c. Representative Plants of P, F₁ and F₂ of the cross Mutant x Thatcher when Spring and Late Spring types have headed. From left to right; Mutant, F₁ Mutant x Thatcher, F₂ Winter, F₂ Late Spring, F₂ Spring and Thatcher.



1-d. Representative plants of P, and F₁ of the cross Thatcher mono IX x Mutant when the Late Spring types have headed. From left to right: Mutant, F₁ Winter def Mono, F₁ Late Spring from Mono and Thatcher mono IX.



Plate 2. Representative plants of P, F₁, F₂ of the cross Mutant
x Thatcher when all plants had headed.



From left to right: Mutant, F₁ Late Spring, F₂ Aberrant, F₁ Winter,
F₂ Late Spring, F₂ Spring, Thatcher.

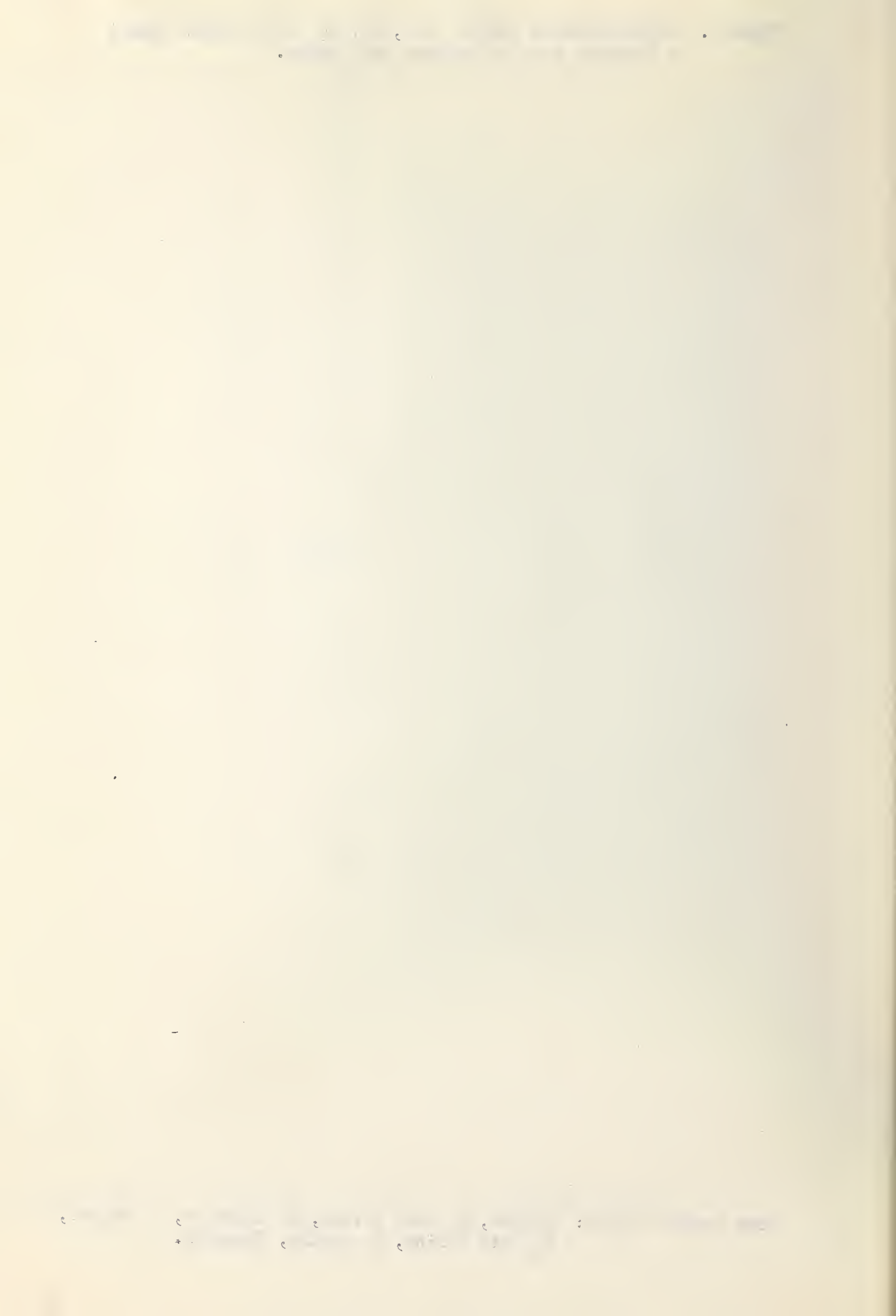


Plate 3. Representative spikes of P, F₁, and F₂ of the cross
Mutant x Thatcher.

REPRESENTATIVE SPIKES OF P, F₁, AND F₂ OF THE CROSS MUTANT X THATCHER



MUTANT

X



THATCHER



F₁ LATE SPRING



F₂ WINTER



F₂ LATE SPRING

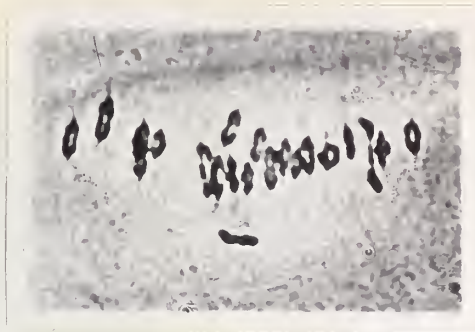


F₂ SPRING

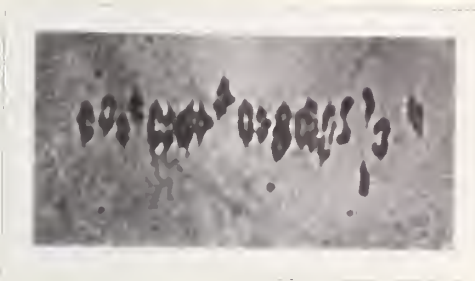


F₂ ABERRANT

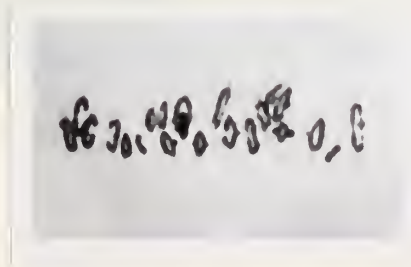
Plate 4. Chromosome behavior at MI in Mutant and F₂ Winter



4-a. Shows 21 bivalents at MI in the Mutant where one bivalent which is off the metaphase plate is very different from the other bivalents.

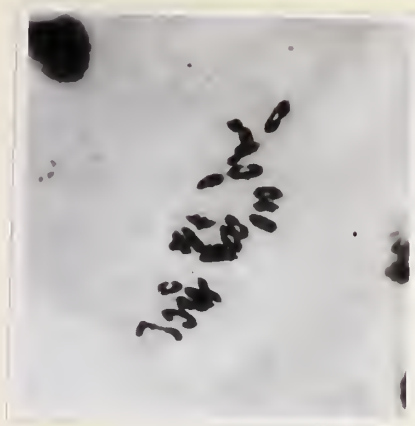


4-b. Shows 21 bivalents at MI in the Mutant where the bivalent referred to in 4-a is pulling apart.



4-c. Shows 20 bivalents and two univalents at MI in the Mutant where the bivalent referred to in 4-a has completely disengaged.

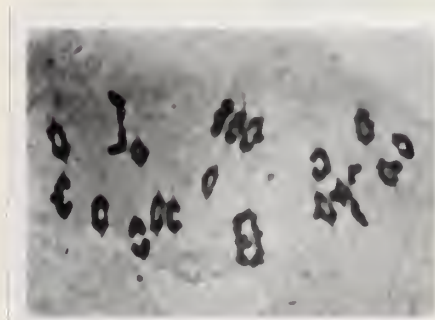
Plate 5. Chromosome behavior at MI in F_1 Late Spring, F_2 Late Spring, and F_1 Late Spring from Mono.



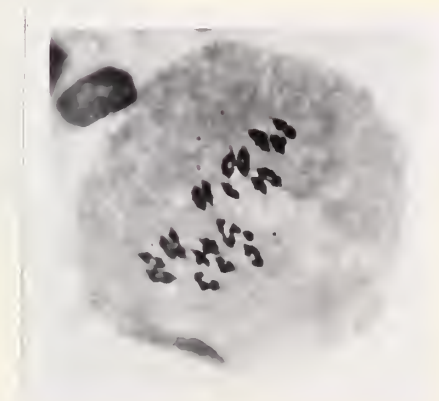
5-a. Shows 21 bivalents at MI in Late Spring types where one open bivalent (at extreme end of metaphase plate) is heteromorphous. The short chromosome in the het. bivalent is presumably from the Mutant, while the long and curved one is from Thatcher.



5-b. Shows 20 bivalents and two univalents off the plate at MI in Late Spring type where the heteromorphous bivalent referred to in 5-a is completely disengaged.



5-c. Shows 19 bivalents and one ring quadri-valent at MI in Late Spring types. The quadri-valent may be an artifact of two open bivalents, the ends of which are appressed to each other.



5-d. Shows 19 bivalents and one open quadri-valent at MI in Late Spring types. The quadri-valent may be an artifact.

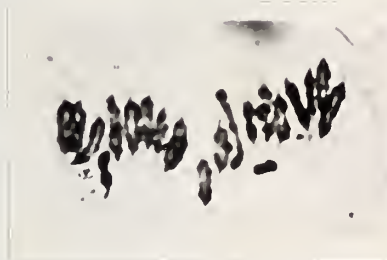
THE JOURNAL OF THE AMERICAN MEDICAL ASSOCIATION
PUBLISHED WEEKLY
CHICAGO, ILL., MAY 1, 1919
Vol. 34, No. 19

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Plate 6. Chromosome behavior at MI and AI in F₁ Winter def Mono



6-a. Shows 20 bivalents and one short univalent at MI in F₁ Winter def Mono where the deficient short univalent is off the metaphase plate and is presumed to have come from the Mutant.



6-b. Shows that the short univalent referred to in 6-a is lagging as a dyad at the equatorial plate during Anaphase I.

Plate 7. Chromosome Morphology and Count in root tip of Mitotic Metaphase.



7-a. Shows 42 chromosomes of mitotic metaphase in root tip in Late Spring type where the deficient chromosome is unidentifiable since there are many chromosomes with short arms.



7-b. Shows 41 chromosomes at mitotic metaphase in root tip in F₁ Winter def Mono where the deficient chromosome is unidentifiable since there are many chromosomes with short arms.

(5) DISCUSSION

(a) Crosses

The morphology of the parents in the crosses were distinct enough to produce an F_1 and F_2 in which the segregants of both crosses could be easily distinguished and classified. However the number of individuals in each type of segregant did not lend itself to simple genetic explanations. But cytological studies of pollen mother cells of the various types of segregants in the two crosses does throw light on the problem.

(b) P.M.C. Cytological Studies

Chromosome behavior in pollen mother cells does give an answer to the type and number of segregants observed.

In the mutant and F_2 Winter segregants the behavior of two similar chromosomes indicate that the same chromosomes are involved causing distinct morphology of winter habit and head characters. Since these two do synapse and form chiasma at least between one pair of arms this pair of chromosome arms may be considered to be homologous.

However no pairing was observed between the other pair of arms. This is most probably due to an extreme deficiency in the homologous portion of similar chromosome arms. While the deficiency does not involve the entire arm, it is probably of sufficient extent that it may be a physical impossibility for chiasma formation to take place.

Identification of these deficient chromosomes was impossible in root-tip studies since there were quite a number of other chromosomes each having a very short arm projecting beyond their centromeres. On the other hand it is positively certain that these short chromosomes in the mutant are not true telocentric chromosomes.

It is possible that in the particular pair of chromosome arms under discussion, chiasma formation does not take place between the deficient arms of the chromosomes probably because crossing over and consequently chiasma formation does not usually take place within this region near the centromeres even in the normal chromosome.

This hypothesis is substantiated by the observations at metaphase I meiosis cells where the short deficient chromosome, when present with the normal homologue which was long, never formed a ring bivalent in F_1 Late Spring, F_2 Late Spring and F_1 Late Spring from mono plants. At the same time and in the same cells the other 20 pairs of chromosomes formed regular ring shaped bivalents even though some of these chromosomes had short arms which were clearly observable in root-tip mitotic metaphase studies, but were not distinguishable in meiotic studies.

Besides the frequent observation of chromosome morphology and configuration already discussed there were other irregularities that have yet to be explained.

The formation of a quadrivalent, an isochromosome with a univalent, a trivalent with a univalent, misdivision of univalents are common in cells of plants of unrelated crosses and between chromosomes that are structurally different. In this study these occurrences are rare and may be ascribed to the physical disturbances in meiosis caused by terminal deficiency in the chromosome pair under discussion.

Cytological observation at meiosis of three of the few aberrant plants, the first from the mutant check row, the second from the F_2 segregants and which headed about the same time as the mutant and the third also from the F_2 segregants and which headed as early as the F_2 Late Spring revealed that they had the same chromosome behavior as, and constitution as the mutant parent or F_2 Winter in the first two cases and as the F_1 Late Spring or F_2 Late Spring in the third case.

It is consequently impossible to explain their occurrence on a genetic or cytologic basis. Nevertheless interference of normal metabolism by cytologically undetectable genes produced by the rare chromosome aberrations observed, cannot be dismissed. Further study of these aberrants is now not possible because they are sterile.

One tentative suggestion might be that gametes and zygotes possessing extreme aberrant chromosomes produced as a result of irregular chromosome behavior are usually inviable. The occasional viable ones would produce weak and sterile plants.

Gametes with terminal chromosome deficiency as in the Mutant may be subject to competition with normal gametes. This is indicated by the F_2 obtained in the cross Mutant x Thatcher in which a ratio of 162 Spring : 209 Late Spring : 26 Winter : 5 Aberrant plants occurred, instead of obtaining a ratio of 1 Spring : 2 Late Spring : 1 Winter plants.

Competitive advantage of gametes with the normal chromosome would result in a ratio in which a much higher than random number of spring : late spring heterozygous plants would be expected. Whether this competitive certation effect is operative only in the male gametes can be determined by reciprocal crossing between the F_1 Late Spring and normal Thatcher.

The morphology and cytology of F_1 Late Spring from Mono and F_1 Winter Mono provide further evidence to back up finding in the parents, F_1 , and F_2 segregants in the cross Mutant x Thatcher.

The long arm of chromosome IX has been proved by several workers to possess the genes for suppression of awning and speltoidy, in the terminal chromosome portion beyond the secondary constriction and the genes regulating growth habit in that sector of the arm proximal to the centromere. Should this be true then the loss of these genes by a fracture of the chromosome arm near the centromere would produce a plant that has winter habit growth, is speltoid and awned.

There is sufficient evidence and justification to conclude that the two short and straight chromosomes that exhibit irregular behavior in the mutant are actually the remains of the homologous chromosomes of chromosome IX, which in the mutant are deficient in the major portion of the long arms. This loss causes the winter habit of growth, extreme speltoidy and full awning observed in the mutant.

Disregarding the twenty normal pairs of chromosomes and concentrating on the one particular pair of chromosome IX it may be said that two doses of the full complement of the two arms, short and long of chromosome IX, as is found in normal Thatcher or F₂ Spring segregants, produces a normal plant having a Spring habit of growth, a fusiform head and apical awning.

The absence of one long arm of chromosome IX causes the plant to head later, the spike to be speltoid and short awned as is found in F₁ Late Spring, F₂ Late Spring and F₁ Late Spring from Mono.

Absence of two long arms of chromosome IX causes winter habit of growth, extreme speltoidy, full awning and slender spikes as in the Mutant.

Absence of one whole chromosome both the long and short arm of chromosome IX causes the plant to behave very much the same as the Late Spring types.

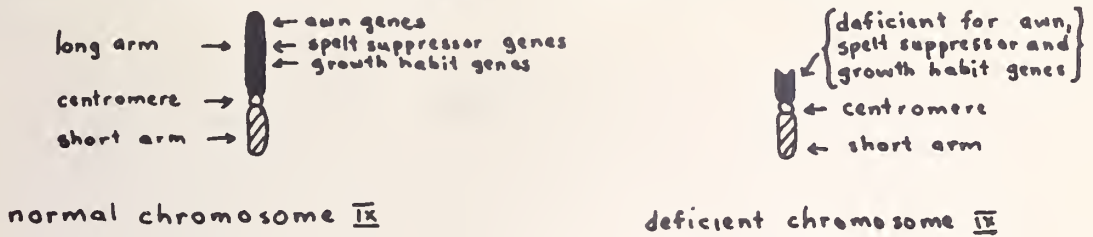
Absence of one whole chromosome IX and also the long arm of chromosome IX, which means a plant monosomic for the short arm of chromosome IX produces a plant that is indistinguishable from that of the Mutant.

A more thorough cytogenetical study is necessary before a greater detailed picture of chromosome IX and its effects could be presented.

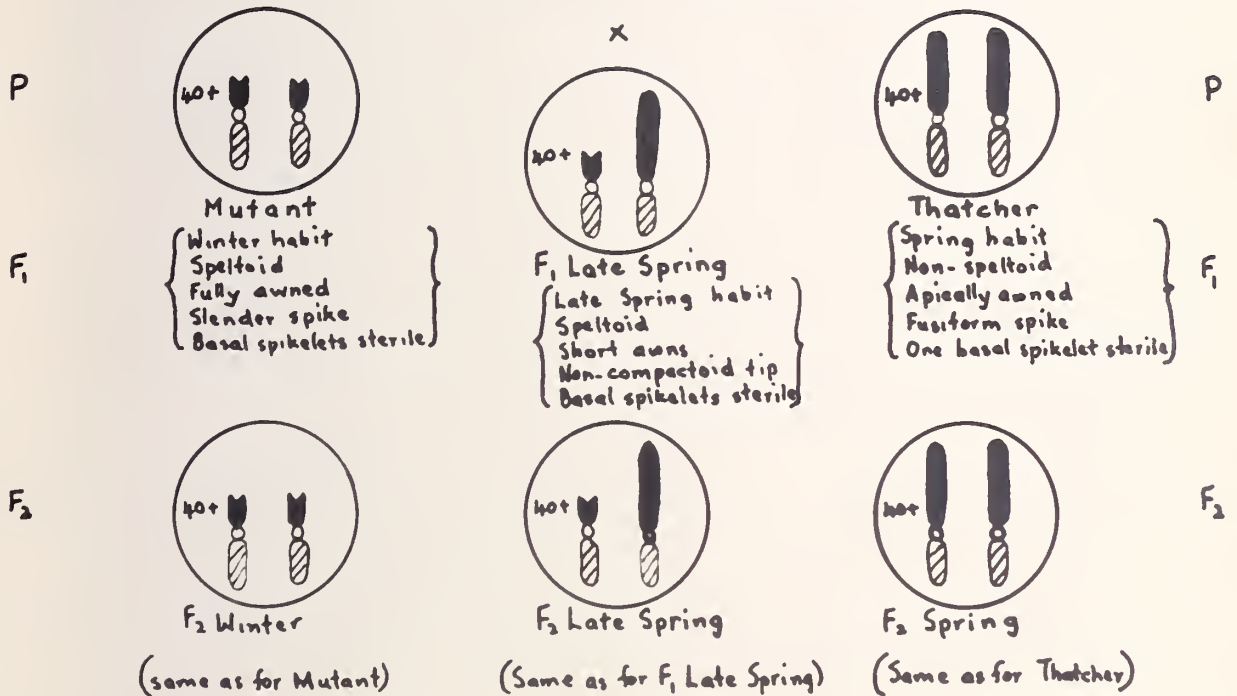
The above discussion of the two particular chromosomes is summarized diagrammatically in Fig. I.

Fig. I

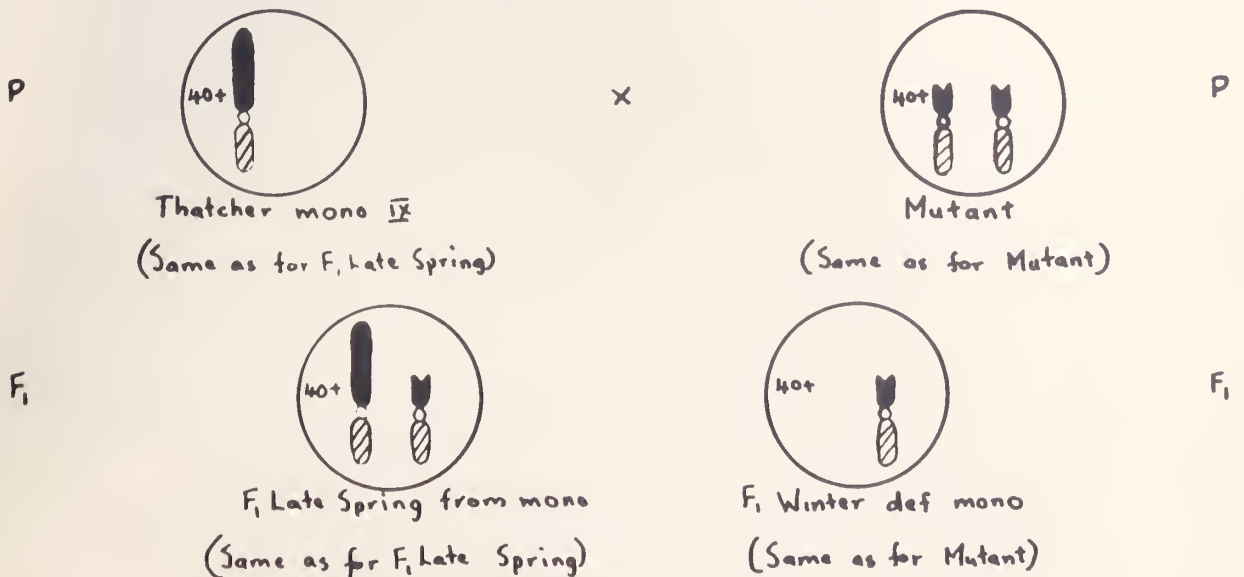
DIAGRAMATIC REPRESENTATION OF CROSSES WITH RESPECT TO GENES AND CHROMOSOMES



(1) MUTANT x THATCHER



(2) THATCHER MONO IX x MUTANT



(c) Root Tip cytological studies

Root tip cytological studies show that they are helpful in determining chromosome numbers at seedling stage and in predicting the type of plant a seedling would grow into. They negate the possibility of telocentric chromosomes and point to the alternative that the characteristic behavior observed between a pair of chromosomes in P.M.C. analyses may be due to a terminal deletion and that the fracture had occurred fairly close to the centromere.

(6) CONCLUSION

This study confirms previous findings in aberrant strains of wheat involving chromosome IX and especially of speltoid and awning inheritance. Although winter segregants in the progeny of speltoids have been observed (Smith et al. 1949) no study was made of those plants. It is very probable that those winter segregants may be very much like the mutant studied here.

The mutant is homozygously deficient for most of the long arm of chromosome IX. This loss is correlated with the winter habit of growth extreme speltoidy and full awning in the spike.

Since no report has been made of wheat plants telocentric for the short arm of chromosome IX, the mutant studied is the closest approach to a plant that is homozygous in a telocentric condition for the short arm of chromosome IX in Thatcher.

(7) SUMMARY

A cytogenetical study was made of a mutant characterised by winter growth habit, extreme speltoidy and full awning. This mutant was found as segregant in the T_2 progeny of T_1 Thatcher wheat seedlings treated with 2,4-D. The other segregants in the same progeny were normals and late speltoids.

Two crosses were made

- (1) Mutant x Thatcher
- (2) Thatcher monosomic IX x Mutant

Cytogenetical analysis confirms previous findings that genes affecting speltoidy awning and habit of growth are on the long arm of chromosome IX.

The Mutant is homozygously deficient for most of the long arm of chromosome IX, and this loss is correlated with the winter growth habit, extreme speltoidy and full awning of the spike.

This deficiency was easily distinguished cytologically in pollen mother cell studies but it was not possible to identify the deficient chromosome in root tip studies since the deficiency was not extensive enough to produce a telocentric chromosome.

The mutant is probably the closest approach so far recorded of a wheat plant that effectively is homozygous for the short arm of chromosome IX in Thatcher.

8. ACKNOWLEDGEMENTS

The author is greatly indebted to the Governors of the University of Alberta for the award of the University of Alberta Fellowship, the World University Service in sponsoring the Fellowship, the Colombo Plan authorities, Canada, in providing funds for transport both ways between Malaya and Canada, to Dr. John Unrau under whose supervision, patience and guidance the study was conducted and manuscript was prepared and with whose recommendation more funds were available from the University to complete this study and to all those in the Plant Science Department of the Faculty of Agriculture who gave help from time to time when needed. To all these institutions and persons the author wishes to express his thanks.

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